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EFFECTS OF SEDIMENT NITROGEN AVAILABILITY AND PLANT DENSITY ON INTERACTIONS BETWEEN THE GROWTH OF *HYDRILLA VERTICILLATA* AND *POTAMOGETON AMERICANUS*

by

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This study examines the growth of *Hydrilla verticillata* (L.f.) Royle and *Potamogeton americanus* C. & S. on both nitrogen-poor and nitrogen-rich sediments and assesses the nature and degree of interspecific interactions between the two species. Extensive greenhouse experiments conducted from May through July 1989 employed sediments differing initially only in sediment nitrogen (fertilized containers: 0.21 ± 0.01 mg exchangeable N per gram dry sediment; unfertilized containers: 0.01 ± 0.00 mg exchangeable N per gram dry sediment). Species were grown monotypically, as well as in 50:50 mixtures, on each sediment type.

Although shoot production did not differ between species in monoculture, shoot production in *Hydrilla* was diminished by 60 to 76 percent in the presence of *Potamogeton*. Likewise, canopy development for *Hydrilla* was reduced in mixtures compared to monocultures, but *Potamogeton* did not show a similar reduction in canopy. High sediment nitrogen increased canopy development by 50 percent in both species. Aboveground biomass for monotypically grown species was similarly low on unfertilized sediment (6 to 8 g per container). However, on fertilized sediment, aboveground biomass in *Potamogeton* (approaching 25 g per

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container) was significantly greater than in *Hydrilla* (approximately 15 g per container). Under both conditions of sediment fertility, *Potamogeton*, in the presence of *Hydrilla*, achieved at least 75 percent of its monotypic aboveground biomass, while *Hydrilla* in mixtures achieved less than 25 percent of the aboveground biomass it exhibited alone. Belowground biomass was twofold greater for both species on unfertilized sediment than on fertilized sediment, yet *Potamogeton* consistently allocated threefold greater biomass to belowground structures than did *Hydrilla*.

In fertilized sediment treatments, exchangeable sediment nitrogen fractions were depleted by 94 to 96 percent in containers supporting *Potamogeton* or mixtures, but only 65 percent of exchangeable nitrogen pools was depleted in containers supporting *Hydrilla*. Patterns of interstitial-water nitrogen were similar to those of exchangeable nitrogen. Sediment fractions of both potassium and phosphorus remained relatively high, regardless of sediment nitrogen fertility or macrophyte species grown. Total plant tissue nitrogen content was an order of magnitude higher in plants grown on fertilized sediment, with *Potamogeton* consistently having a higher tissue nitrogen content than *Hydrilla*.

As a measure of competitive ability, suppression coefficients calculated from biomass data for *Potamogeton* on unfertilized sediment exceeded those for *Hydrilla* by a factor of 4.64. Although *Potamogeton* still outcompeted *Hydrilla*, higher sediment nitrogen reduced *Potamogeton*'s advantage to a factor of 2.86. Based on results of this study, it is postulated that *Potamogeton* should displace *Hydrilla* when sediment nitrogen is in short supply.

14. (Concluded).

Aquatic plants	Macrophyte
Biomass	Nitrogen
Density	Production
Interspecific interaction	Sediment

Contents

iii

Preface

The work reported herein was conducted as part of the Aquatic Plant Control Research Program (APCRP), Work Unit 32351. The APCRP is sponsored by the Headquarters, US Army Corps of Engineers (HQUSACE), and is assigned to the US Army Engineer Waterways Experiment Station (WES) under the purview of the Environmental Laboratory (EL). Funding was provided under Department of the Army Appropriation No. 96X3122, Construction General. The APCRP is managed under the Environmental Resources Research and Assistance Programs (ERRAP), Mr. J. L. Decell, Manager. Mr. Robert C. Gunkel was Assistant Manager, ERRAP, for the APCRP. Technical Monitor during this study was Mr. James W. Wolcott, HQUSACE.

Principal Investigator for the study was Dr. John W. Barko, Aquatic Processes and Effects Group (APEG), EL. The report was prepared by Dr. Nancy J. McCreary, currently of the Department of Biology, Lafayette College, Easton, PA, with contributions from Ms. Dwilette G. McFarland and Dr. Barko of the APEG. Experimental design, data analysis, and interpretation were provided by the authors. Technical assistance from the APEG was provided by Mmes. Gail A. Bird, Wanda A. Dee, Evelyn C. Henderson, and Monica N. Humphrey and Messrs. Harry L. Eakin, Kevin R. Pigott, and F. Ashley Boyd. The report was reviewed within EL by Drs. William D. Taylor and Craig S. Smith.

This study was performed under the supervision of Dr. Richard E. Price, Chief, APEG; Mr. Donald L. Robey, Chief, Ecosystem Research and Simulation Division; and Dr. John Harrison, Chief, EL.

COL Larry B. Fulton, EN, was Commander and Director of WES. Dr. Robert W. Whalin was Technical Director.

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1 Introduction

The responses of submersed aquatic macrophytes to physical and chemical gradients in the water column have been widely studied (for synthesis, see Smart 1990). These studies have focused on major limnological parameters affecting growth, including light, dissolved carbon, and some cations, notably potassium (Barko 1982, Barko et al. 1988). However, the mineral nutrition of rooted aquatic macrophytes is derived largely from nutrient pools, especially nitrogen and phosphorus, in sediment (Carignan and Kalff 1980; Barko and Smart 1986; Barko, Smart, and McFarland 1991). The availability of sediment nutrients may be affected by sediment texture and chemical composition (Denny 1980, Smart and Barko 1985, Barko and Smart 1986), as well as by direct root uptake of sediment nutrient reserves (Barko et al. 1988). Recent investigations have demonstrated that even species with relatively small root systems can effectively reduce nitrogen and phosphorus pools in sediment, thereby imposing potentially limiting conditions on subsequent macrophyte growth (Barko et al. 1988, Chen and Barko 1988).

Thus far, much research has examined the effects of sediment on the nutrition of individual submersed macrophyte species, while impacts of sediment nutrients on multispecies assemblages and species interactions remain relatively unknown. Predicting the outcome of interspecific competition generally depends upon knowledge of individual species' responses (McCreary and Carpenter 1987, Smart and Barko 1989), preferably using multiple initial densities of individuals (Inouye and Schaffer 1981, McCreary and Carpenter 1987). Single species' responses provide an expectation of success against which responses of mixtures can be measured. Likewise, the use of multiple initial densities provides information on how abundance may affect competitive success.

Potamogeton americanus C. & S. (= *P. nodusus* Poiret) is a relatively common, innocuous pondweed native to North America. It typically provides support for aquatic insect communities and is attractive as a food source for a variety of waterfowl (Fassett 195*i*). In contrast, *Hydrilla verticillata* (L.f.) Royle is an invasive, exotic species, introduced in Florida around 1960 (Langeland, Thayer, and Laroche 1989). *Hydrilla* has since spread to a variety of aquatic habitats in the southeastern United States, and its presence has been documented in California as well (Dechoretz

1989). Proliferation of *Hydrilla* can cause severe water-use problems and may lead to the displacement of native vegetation (Langeland, Thayer, and Laroche 1989).

Although the biology of both *Hydrilla* and *Potamogeton* has been variously studied, there has been no research to date on competitive interactions of this particular species pair, even though some studies invoke *Hydrilla*'s competitive superiority as the mechanism of native species displacement (Haller and Sutton 1975; Van, Haller, and Bowes 1978). This report presents the results of an investigation designed to examine the influences of sediment fertility on the growth of *Hydrilla* and *Potamogeton* in single- and mixed-species cultures. The report is intended to augment current understanding of effects of sediment nitrogen availability on the growth of submersed macrophytes and, further, to identify growth responses affected by nitrogen availability and potentially influencing the outcome of interactions between these two important macrophyte species.

2 Materials and Methods

The study was conducted in a greenhouse facility at the US Army Engineer Waterways Experiment Station (WES) in Vicksburg, MS. Culture solution in twelve 1,200-L fiberglass tanks was prepared according to Smart and Barko (1985) to yield the following elemental composition (mg/L):

Na^+ = 16.0, K^+ = 6.0, Ca^{+2} = 25.0, Mg^{+2} = 6.8, HCO_3^- = 51.8,

Cl^- = 44.2, SO_4^{+2} = 26.9. The tanks were individually maintained with water temperatures of 25 $\pm$ 2 $^{\circ}$C. The greenhouse was covered with a 73-percent neutral-density shade fabric that reduced maximum midday PAR (photosynthetically active radiation) to about 500 $\mu E/m^2/sec$.

Preparation of Sediments and Species

Two levels of nitrogen fertility were prepared using sediment dredged from Brown's Lake, WES (detailed composition found in Barko and Smart 1986). The low sediment nitrogen level was obtained by using previously planted sediment (referred to as unfertilized sediment). To obtain the high sediment nitrogen level, fresh, unplanted sediment was amended with 0.8 g NH_4Cl/L, thereby increasing sediment nitrogen by approximately an order of magnitude.

Apices of 6-week-old *Hydrilla* were clipped 15 cm in length from the WES continuous greenhouse stock. This stock (maintained on fresh, unamended Brown's Lake sediment) was originally established from dioecious plants collected in Lake Seminole, Florida. Dormant rhizomes of *Potamogeton* were obtained commercially from a wildlife nursery in Oshkosh, WI, and germinated in the laboratory to ensure viability and size uniformity.

Experimental Design and Execution

The experimental design was a modified 2 × 2 × 3 factorial design: two sediments, fertilized or unfertilized; two densities, high or low; and three species-ratio treatments, *Hydrilla* monoculture, *Potamogeton* monoculture, or dual-species mixture. Both monocultures and 50:50 mixtures were provided at two densities, either 8 or 16 plants per container. Containers of dimensions 24 by 24 by 10 cm deep were filled with approximately 4 L of well-mixed sediment, and plants were spaced evenly within each. In mixtures, the arrangement was alternated by species. Once planted, the sediment surface was covered with a thin layer of washed silica sand. Six replicate containers were planted for each sediment type/density combination and placed in prepared tanks. Each tank, therefore, supported containers of a single sediment fertility and a single density level for a single species-ratio treatment.

The study was begun on 19 May 1989. Tanks were monitored daily for temperature, and minor adjustments were made as necessary. At weekly intervals, pH and conductivity of the culture solution were determined, along with concentrations of major cations (Ca^{+2}, Mg^{+2}, Na^+, and K^+), measured using flame atomic absorption photometry (AA) on acidified samples.

Inflorescence spikes of *Potamogeton* were counted by tank after approximately 6 weeks. At the same time, light extinction coefficients were determined in each experimental tank according to Wetzel (1983) using a Li-Cor cosine quantum radiometer photometer. Measurements were made at 35 cm below and incident to the water surface.

On 27 June 1989, the experiment was dismantled. Within each container, aboveground biomass was clipped at the sand surface and separated by species in mixture treatments. Total stem number, maximum stem length, and canopy height (i.e., midpoint of the most dense 10-cm segment of plant shoots) were determined immediately. Number of floating leaves was also determined for *Potamogeton*. In addition to aboveground biomass, belowground biomass was recovered from one half of each container by rinsing with water through a 1-mm mesh sieve. All plant materials were weighed after drying to constant mass (at 80 °C) and analyzed for tissue nutrients. The remaining sediments were cored to obtain six replicate samples for the analysis of final levels of sediment nutrients. Procedures used for both plant tissue and sediment nutrient analyses are described in the following section.

Nutrient Analyses

Although sample preparation differed for plant and sediment material, the resulting extracts or digests were processed similarly to obtain nitrogen, phosphorus, and potassium levels.

Initial plant tissue nutrients were determined on six replicate apical sprigs of *Hydrilla* or three replicate germinated rhizomes of *Potamogeton*. Plant tissues (oven-dried at 80 °C) were finely ground, and digested with sulfuric acid and hydrogen peroxide. The resulting digest was subsequently analyzed for potassium using AA. Nitrogen and phosphorus were measured using a Technicon autoanalyzer, employing a molybdate method for phosphorus and a salicylate method for nitrogen (APHA 1985). Final tissue nutrient levels were obtained similarly for all six replicates of both aboveground and belowground tissues.

For initial sediment nutrient levels, moisture content and bulk density were determined on three replicate samples; these data were used in the calculation of exchangeable ammonium, exchangeable potassium, and extractable phosphorus. Six replicate samples each of fertilized and unfertilized sediments were extracted with NH_4Fl, and the resulting extract was measured for phosphorus using a molybdate method on a Technicon autoanalyzer. An additional six replicate samples of each sediment were processed with NaCl in a cation exchange procedure. This extract was subsampled to obtain exchangeable ammonium measured by a salicylate method on a Technicon autoanalyzer, as well as exchangeable potassium, determined directly using AA.

Replicate samples of each sediment (n = 6) were centrifuged to obtain interstitial water. Dissolved nitrogen, phosphorus, and potassium were then determined using the same analytical methods. Upon completion of the experiment, both interstitial and exchangeable nutrient fractions were determined in sediments remaining in each of the six replicate containers.

Data Analyses

Data were analyzed on a VAX mainframe computer using the Statistical Analysis System (SAS Institute 1988). All means reported herein are arithmetic averages ±1 standard error of the mean. Generally, replicate sediment flats within a single tank were considered experimental units. Analysis of variance was determined where appropriate using the general linear models procedure; normality of residuals was confirmed using normal probability plots. Comparisons of means tests could have been employed to identify the magnitude of significant main effects, but were not needed given the two- or three-level design for main effects. Statistical significance of both main effects and interactions was evaluated as a probability of obtaining a similar F-value by chance of 5 percent or less. Hereafter,

statements of statistical significance without precise indication of probability level refer to $P < 0.05$.

Root-to-shoot mass ratios were calculated for monospecific cultures. By adjusting total biomass in monocultures for the total number of shoots and incorporating root-to-shoot ratios, the average biomass profile of a single monospecifically grown plant could be estimated. In addition, tissue nitrogen concentrations were weighted by biomass to assess nitrogen content within experimental containers.

Least-squares linear regressions of plant tissue nitrogen content as a function of nitrogen content remaining in sediments were performed using the REG procedure (SAS Institute 1988). Regressions employed data from fertilized sediment treatments, for both interstitial and exchangeable sediment nutrient fractions.

Suppression coefficients for each species were calculated to summarize competitive effects in mixtures relative to growth of plants alone. Developed by Aarssen (1985), the suppression coefficient (S) enables comparison of the biomass of Species A when in the presence of Species B to the biomass of the same number of Species A grown alone. It therefore indicates the degree to which the growth of Species A is suppressed by the presence of Species B. If a species is unaffected by its neighbor, the value of S approaches unity. The yield suppression ratio (YSR) relates S of the more-suppressed species to S of the less-suppressed species, expressed as a simple quotient. The YSR should increase as the difference between competitors declines.

3 Results

Morphological Responses

Hydrilla grown alone produced the same number of shoots regardless of sediment fertility, yet was sensitive to the initial planting density (Figure 1), with about one third more shoots established in the high-density treatment. In contrast, *Potamogeton* produced more shoots on fertilized sediment, with shoot production relatively insensitive to initial density. On the unfertilized sediment, shoot production did not differ substantially between species; however, on fertilized sediment, the number of shoots established by *Potamogeton* was about twice that of *Hydrilla*.

For both species, shoot production was greater in monoculture than in mixture (Figure 1). When grown in mixture, *Potamogeton* produced approximately 73 percent of the number of shoots it produced in monoculture. In contrast, *Hydrilla* in mixture produced only about 32 percent of the shoots it produced alone.

As shown in Figure 2, *Potamogeton* exhibited greater potential for stem elongation than did *Hydrilla* ($F = 83.46$; $P < 0.0001$), yet the influence of species on maximum shoot length in monocultures was dwarfed by the magnitude of response to the sediment manipulation ($F = 2,174.4$; $P = 0.0000$). Likewise, the height of the canopy responded strongly to fertilized sediment, with the species differential being relatively less pronounced ($F = 4,236.22$; $P = 0.0000$, and $F = 90.29$; $P < 0.0001$, respectively).

Under corresponding treatments, *Potamogeton*'s canopy was as tall as, or taller than, that of *Hydrilla* (Figure 2). In mixtures, canopy height in *Potamogeton* was similar to monospecific responses. *Hydrilla*, however, had significantly shorter stature in mixtures on unfertilized sediment, but exhibited similar canopy height between monocultures and mixtures on fertilized sediment.

Light extinction coefficients measured just prior to harvest reflected substantial canopy formation by both species on fertilized sediment. However, light availability under *Potamogeton* was less than that found under

well-developed monotypic *Hydrilla* (9.955 ± 3.914 versus 4.797 ± 1.399, respectively). The extinction coefficient for mixtures was intermediate (6.872 ± 2.603).

Floating leaves and inflorescence spikes were formed by *Potamogeton* only on fertilized sediment. More floating leaves were produced per initial *Potamogeton* plant in the presence of *Hydrilla* than were produced when alone (Table 1). Likewise, *Potamogeton* grown alone formed fewer inflorescence spikes than it did when grown with *Hydrilla* (Table 1).

Biomass Production

Aboveground biomass (Figure 3) was affected to a greater extent by sediment fertility ($F = 606.15$; $P < 0.0001$), by species differences ($F = 427.49$; $P < 0.0001$), and by species-sediment interaction, i.e.. the influence of sediment fertility on species' responses ($F = 241.69$; $P < 0.0001$), than by initial plant density ($F = 14.24$; $P < 0.001$). Basically, aboveground biomass was similar in both species grown monotypically on unfertilized sediment. However, fertilized sediment increased the differential between species; that is, under these conditions, aboveground biomass in *Hydrilla* was nearly double, while that in *Potamogeton* was more than triple (3.5 times) the aboveground biomass accrued on unfertilized sediment.

Under both conditions of sediment fertility, aboveground biomass in the mixtures was dominated by *Potamogeton* (Figure 3). Overall, *Potamogeton* in the presence of *Hydrilla* accrued at least 75 percent of its monotypic aboveground biomass, while *Hydrilla* in the mixtures achieved less than one quarter the aboveground biomass it exhibited alone.

Neither species allocated belowground biomass differently in response to density, yet both increased belowground production by twofold on unfertilized sediment (Figure 4). *Potamogeton* consistently allocated three times more biomass below ground than did *Hydrilla* ($F = 70.24$; $P < 0.0001$). Although mixtures could not be separated by species, belowground biomass appeared to predominantly reflect allocation patterns of *Potamogeton*.

Root-to-shoot ratios in monoculture were influenced primarily by species ($F = 473.07$; $P < 0.0001$), by sediment fertility ($F = 393.21$; $P < 0.0001$). and by species-fertility interaction ($F = 285.35$; $P < 0.0001$). The most important effect of increased density on biomass allocation in this study was a decrease in aboveground biomass per *Hydrilla* plant on fertilized sediment (Figure 5). Overall, the root-to-shoot ratio (expressed as a grand mean) for *Potamogeton* was 0.47 compared to 0.12 for *Hydrilla*.

8

Nutrient Allocation

Tissue nitrogen concentrations (on a per gram dry mass basis) were unaffected by initial density but were considerably higher in both species on fertilized, as opposed to unfertilized, sediment (Figure 6). On fertilized sediment, *Potamogeton* and *Hydrilla* each exhibited higher nitrogen concentrations in aboveground than belowground tissues. However, on unfertilized sediment, variations in nitrogen levels for both species were less pronounced, with somewhat higher nitrogen levels in aboveground tissues of *Potamogeton*, and in belowground tissues of *Hydrilla*. Under both conditions of sediment fertility, tissue nitrogen concentrations in monotypically grown plants were similar to those in mixtures.

Aboveground nitrogen content (i.e., the product of nutrient concentration and plant mass) was unaffected by initial density (Figure 7). Sediment fertility elicited the greatest response in nitrogen content (F = 2,173.34; P = 0.0000), with about an order of magnitude more nitrogen in aboveground tissues of both species grown on fertilized sediment. Under those sediment conditions, *Potamogeton* accumulated significantly more nitrogen than did *Hydrilla* (F = 673.33; P = 0.0000) and dominated patterns of nitrogen accumulation in mixtures.

Belowground nitrogen content was insensitive to either density or sediment fertility, but was significantly affected by species (F = 40.12; P < 0.0001). *Potamogeton* consistently allocated more nitrogen to belowground tissues than did *Hydrilla* (Figure 8). Although somewhat variable, mixtures reflected patterns of nitrogen accumulation in *Potamogeton* more closely than in *Hydrilla*.

Tissue nitrogen concentrations were used to assess the nitrogen cost per gram dry biomass produced on unfertilized sediment. Aboveground tissue nitrogen cost for *Potamogeton*, at 9.18 mg N/g tissue, significantly exceeded *Hydrilla* nitrogen cost, at 7.17 mg N/g tissue (F = 23.95; P < 0.0001). These values were offset in both species by significantly different belowground nitrogen costs of 9.55 mg N/g tissue for *Hydrilla*, and 7.08 mg N/g tissue for *Potamogeton* (F = 20.30; P = 0.0002). However, when normalized for proportionate allocation to root and shoot components, overall nitrogen cost for a given gram of total plant biomass did not differ between species. For *Potamogeton*, overall nitrogen cost was 7.502 mg N/g plant, compared with 7.734 mg N/g plant for *Hydrilla* (F = 0.37; P = 0.5481).

Sediment Nutrient Uptake

Initial potassium levels did not differ substantially between fertility treatments for exchangeable fractions (fertilized, 0.15 ± 0.00 mg/g dry sediment; unfertilized, 0.13 ± 0.01 mg/g dry sediment) or interstitial

water fractions (fertilized, 19.9 ± 0.60 mg/L; unfertilized, 12.7 ± 0.91 mg/L). By the conclusion of the experiment, exchangeable potassium was still plentiful across all treatments, particularly in unfertilized sediment (Figure 9). Although slightly less exchangeable potassium remained in fertilized sediments, it did not differ by species. A similar pattern was evident for potassium in sediment interstitial water by the end of the experiment (Figure 10).

Initial exchangeable phosphorus was slightly lower in the unfertilized sediment (0.10 ± 0.00 mg/g dry sediment) compared with the fertilized sediment (0.14 ± 0.00 mg/g dry sediment), while initial interstitial phosphorus levels did not differ between the two treatments (unfertilized, 0.80 ± 0.06 mg/L; fertilized, 0.90 ± 0.00 mg/L). Final levels of exchangeable phosphorus were not appreciably different between species or fertility treatment (Figure 11), and interstitial levels nearly always exceeded 0.10 mg/L (Figure 12).

Exchangeable nitrogen differed initially between sediment treatments by a factor of 18. By the conclusion of the study, exchangeable nitrogen remaining in unfertilized treatments was 26 to 32 percent of the initial nitrogen present (Table 2) and did not vary significantly by species. Exchangeable nitrogen remaining in fertilized sediment was 4 and 6 percent, respectively, for *Potamogeton* monocultures and mixtures; nitrogen remaining in fertilized sediment supporting *Hydrilla* monocultures was about 35 percent.

Nitrogen remaining in the interstitial water of unfertilized sediment was about 6 to 9 percent of that contained in the initial pool and, similar to patterns of exchangeable nitrogen, demonstrated no significant differences due to species (Table 3). However, in fertilized sediment supporting *Hydrilla*, 24 percent of the initial interstitial water nitrogen remained, compared with only 1 to 3 percent remaining in monocultures of *Potamogeton* and mixtures, respectively.

Least-squares regressions of total plant nitrogen content over final interstitial-water or exchangeable nitrogen fractions in fertilized sediment showed significant, negative relationships only for *Hydrilla* (Y = 789.51 - 11.38 X ; r^2 = 0.5367 , P = 0.0067 for interstitial nitrogen; Y = 673.02 - 1,923.56 X ; r^2 = 0.5367, P = 0.0284 for exchangeable nitrogen). *Potamogeton* tissue nitrogen was unrelated to nitrogen left in the fertilized sediment.

Interspecific Suppression

Potamogeton maintained a very high suppression coefficient under both sediment fertility conditions (Figure 13). *Hydrilla* showed considerable suppression of growth, although it was more suppressed on unfertilized than fertilized sediment. On a per plant aboveground yield basis, one *Potamogeton* plant on unfertilized sediment was equivalent to 4.64 *Hydrilla* plants

10

under the same sediment conditions. That difference was less striking on fertilized sediment, where one *Potamogeton* plant was equivalent to 2.86 *Hydrilla* plants. The yield suppression ratio in this study increased as sediment fertility increased (Figure 13).

4 Discussion

Responses to Density

A long-standing criticism of plant competition experiments has been the use of a single initial plant density, which may bias the outcome of competition (Torsell and Nicholls 1976, de Benedictus 1977, Inouye and Schaffer 1981). Additionally, some measures of competitive superiority may be more sensitive than others to initial plant density (for review, see Rousch et al. 1989). However, initial plant density overall had a relatively minor effect on results obtained in the present investigation. Thus, our data indicate that the use of multiple initial densities may not be necessary in some competition experiments. In greenhouse or laboratory studies where a nutrient is present in a finite volume of sediment, the initial density of plants appears inconsequential to biomass accumulation (Sutton, Littell, and Langeland 1980), and therefore may not directly influence competitive outcome. However, in a natural setting, where nutrient inputs and losses may vary, or where multiple growing seasons contribute to density-dependent mortality (McCreary and Carpenter 1987), the density of potential competitors may be an important complexity to be considered.

The only clear responses to initial plant density in this study were displayed by monocultures of *Hydrilla* grown on fertilized sediment. Under these conditions, *Hydrilla* at low density maximized individual plant biomass by maintaining fewer shoots, with presumably greater access to sediment nutrients and available light. Total biomass of this species on fertilized sediment was slightly greater at high than at low density. However, in the high-density treatment, shoots were elongated, with less biomass per individual shoot. These plastic responses in *Hydrilla* suggest a high degree of intraspecific regulation of growth form, and in general, may reflect potential populational adjustments to changing light and sediment conditions.

Responses to Sediment Nutrients

The responses attributed here to low sediment nitrogen reserves might have been related to limiting levels of other nutrients, notably phosphorus or potassium. Our sediment nutrient analyses indicate, however, that substantial resource pools of both elements remained in sediments that had supported plant growth. It is not surprising that potassium remained plentiful, since studies have demonstrated that the overlying water column provides the major source for potassium uptake in rooted submersed macrophytes, and the culture medium used in our experiment provided an ample supply of potassium (Barko 1982, Smart 1990).

Plentiful phosphorus reserves in sediment as well as higher than expected tissue phosphorus levels (McCreary and Barko, unpublished data) for both species rule out phosphorus as a limiting factor to growth in this experiment. However, where sediment nitrogen was initially low, tissue nitrogen concentrations for both species, in mixture and in monocultures, were 1 percent or less—well below the 1.3-percent critical concentration level considered limiting for some aquatic macrophytes (Gerloff and Krombholz 1966). Although the study reported herein did not attempt to precisely determine critical concentrations, it did provide ample evidence for nitrogen-limited growth on unfertilized sediment.

While differences in responses to sediment fertility generally dominated our findings, differences between species were often striking. Data from mixtures clearly showed that *Potamogeton* was more efficient than *Hydrilla* at incorporating sediment nitrogen into shoot tissues, regardless of the presence of a competitor or the degree of sediment fertility. However, on unfertilized sediment, a decided advantage over *Hydrilla* was conferred to *Potamogeton* through its greater production of root mass, at relatively low nitrogen cost. Increased belowground biomass allocation potentially enhances access to sediment nutrients, and therefore is an important response to nutrient limitation (Denny 1972, Anderson 1978, Barko and Smart 1986, Hunt and Nicholls 1986). While *Hydrilla* also responded to sediment nitrogen shortage by increased root biomass, its rooting system was far less extensive than that of *Potamogeton*, as indicated by the fourfold difference in root-to-shoot ratios. Patterns of monotypic biomass allocation thus suggest that *Potamogeton* may effectively outcompete *Hydrilla*, particularly when sediment nitrogen is in short supply.

Although overall plant nitrogen cost did not differ between species when nitrogen was limiting, different patterns of allocation favored the more conservative growth form (i.e., greater belowground allocation) of *Potamogeton*. A previous study by Smart and Barko (1989) based predictions of competitive outcomes on nitrogen cost of aboveground tissues. *Vallisneria americana* required twice as much nitrogen for shoot tissues as *Hydrilla*, and was therefore predicted to be disadvantaged when nitrogen was in short supply. However, when species allocate substantial mass to belowground structures, as do *Potamogeton* and *Vallisneria*, aboveground

nitrogen cost alone cannot accurately predict competitive outcomes. Had we only assessed aboveground nitrogen costs in this study, we would have missed how *Potamogeton*'s nitrogen-cheap belowground tissues can offset the high nitrogen cost of aboveground tissue and impact the prediction of competitive superiority.

The least-squares regressions performed on fertilized sediment in this study revealed some interesting information regarding sediment nitrogen use in these two species. If we assume that most of the nitrogen lost from the sediment was incorporated into plant tissue, we would expect a negative relationship between the nitrogen content of tissues and nitrogen left in the sediment, particularly when plenty of nitrogen uptake occurred, i.e., on fertilized sediment. *Hydrilla* demonstrated this expected relationship; for *Potamogeton*, however, more nitrogen was depleted from fertilized sediment than could be accounted for in plant tissues. These findings thus raise questions about possible nitrogen-depleting mechanisms in *Potamogeton* which may be lacking in *Hydrilla*.

Oxygen release in a number of vascular plants has been shown to substantially alter redox of the sediment rhizosphere (Carpenter, Elser, and Olson 1983), thereby mediating transformations of nutrients such as phosphorus and iron (Jaynes and Carpenter 1986). This phenomenon of oxygen release by macrophytes enables nearby reduced ammonium nitrogen to diffuse into the rhizosphere; there it is oxidized to nitrate, and eventually converted to nitrogen gas, which is subsequently lost from the plant through the lacunar system (Reddy and Patrick 1984; Reddy, Patrick, and Lindau 1989). This mechanism can generate as much as 34 percent loss of nitrogen from the sediment. Since conspecifics of *P. americanus* such as *P. perfoliatus* have been shown to release oxygen to sediments (Kemp and Murray 1986), it is possible that this mechanism may explain the observed loss of sediment nitrogen and its relationship to plant tissue nitrogen in our study. If *P. americanus* does, in fact, oxidize sediment and thereby mediate changes in sediment nitrogen through nitrification-denitrification processes, not only does it maintain a more effective nitrogen-use mechanism for itself (as evidenced here by nitrogen accumulation patterns), but it may adversely affect the use of this element by a potential competitor.

Responses to Competitors

If *Hydrilla* and *Potamogeton* were competitively equivalent, each would exhibit a 50-percent contribution to mixtures consisting of equal numbers of initial propagules. However, responses in mixtures consistently reflect dominance by *Potamogeton*. For new shoots formed within a given density or fertility treatment, *Potamogeton* in the presence of *Hydrilla* achieved about 70 percent of monospecific responses. In contrast, *Hydrilla* in mixtures displayed responses at about 20 percent of monotypic levels. Further, *Potamogeton*'s canopy formation and elongation in

14

mixture did not differ from that in monocultures, while the presence of *Potamogeton* under nitrogen-limiting conditions was a striking impediment to the ability of *Hydrilla* to form a canopy.

Previous studies (Haller and Sutton 1975; Van, Haller, and Bowes 1978) have documented extensive canopy formation in *Hydrilla*, and inferred some degree of competitive superiority for *Hydrilla* as a result. However, the degree to which *Potamogeton* extinguished light in the present investigation clearly exceeded that of *Hydrilla*. *Potamogeton* also generated far more floating leaves per plant when grown with *Hydrilla* than when grown alone. This could represent a plastic morphological response by *Potamogeton* to the presence of *Hydrilla* as a potential competitor.

Potamogeton's competitive superiority was most dramatically seen in aboveground biomass dynamics. On unfertilized sediment, where both species accumulated only about 8 g of mass, mixtures were dominated by *Potamogeton*. In spite of *Hydrilla*'s increased biomass accumulation on fertilized sediment, mixtures were predominantly *Potamogeton*. Although belowground mass dynamics were inseparable by species in mixture, accumulation was more than likely due to *Potamogeton*, owing to prevailing patterns in monocultures.

Trends in aboveground mass were used in the estimation of Aarssen's (1985) suppression coefficient, which was much lower for *Hydrilla* than for *Potamogeton*. Interestingly, differences between the species declined with sediment nitrogen addition. The competitive edge held by *Potamogeton* when nitrogen was limiting diminished as sediment nitrogen was more plentiful, as evidenced by the increased YSR.

The decline in *Potamogeton*'s competitive superiority with higher sediment nitrogen also has implications for reproductive potential. *Potamogeton* formed substantially more inflorescence spikes in the presence of *Hydrilla*, thereby ensuring greater potential for sexual reproduction. Sexual propagation is energetically and nutritionally costly (Sculthorpe 1967), yet may represent an investment in the advantage of genetic variation to future populations. Germination may occur in a more competitively favorable environment, or offspring from a sexual union might be better adapted for direct conflicts with a competitor.

5 Conclusions and Recommendations

The results of this study and others (Stewart 1988, Smart and Barko 1989) provide no evidence for *Hydrilla verticillata* as a competitively superior species, and in fact, demonstrate the ability of a native species, *Potamogeton americanus*, to outcompete and potentially displace this exotic nuisance species under nitrogen-limiting conditions. The success of *Potamogeton* over *Hydrilla* in this study was independent of density. It was concluded, therefore, that in greenhouse or laboratory studies where sediment nutrients are in finite supply, initial density of plants is inconsequential to biomass accumulation, and thus probably does not influence competition directly.

When mechanisms of sediment nitrogen use are closely examined, a potential advantage is conferred to *Potamogeton*. If *Potamogeton* can oxidize sediments and mediate changes in sediment nitrogen through nitrification-denitrification processes, it may be able to adversely affect nitrogen use by a potential competitor. This mechanism presents a possible explanation for the observed dominance of *Potamogeton* over *Hydrilla* in species mixtures. We recommend further studies be conducted to better elucidate sediment nitrogen transformations and use by both native and exotic species.

The role of a floating-leaf canopy, such as that generated by *Potamogeton*, may have contributed to the observed dominance of *Potamogeton* in our study. Thus, further studies among different styles of canopy-forming species might elucidate the relative importance of competition for sediment nutrients. Such studies, on both sediment nitrogen transformation and canopy formation, may enable us to establish a hierarchy for different species of aquatic macrophytes over a range of sediment fertility states, thereby allowing managers to more accurately predict changes in macrophyte abundance patterns as sediment nitrogen supply varies.

The increasingly common occurrence of *Hydrilla* in North American waterways clearly indicates that additional factors may also be involved in the associated loss of native species. Studies are needed to further advance

our understanding of the complex mechanisms governing growth of submersed aquatic macrophytes. Better information on these mechanisms will ultimately increase flexibility in managing submersed aquatic vegetation.

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18

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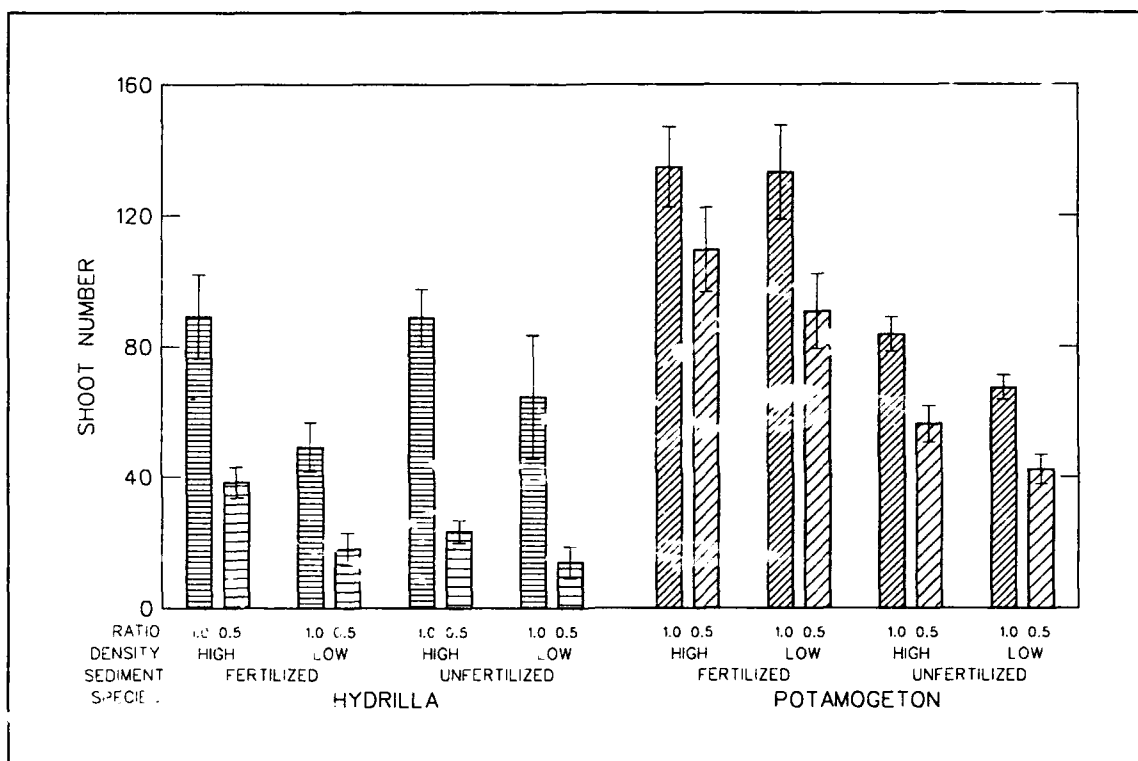
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Figure 1. Shoot number in *Hydrilla* and *Potamogeton* grown on fertilized or unfertilized sediment. Ratios of 1.0 indicate monoculture responses, while ratios of 0.5 indicate mixture responses at both high (n = 16) and low (n = 8) initial plant density. Each bar is the mean ±1 standard error of six replicate flats
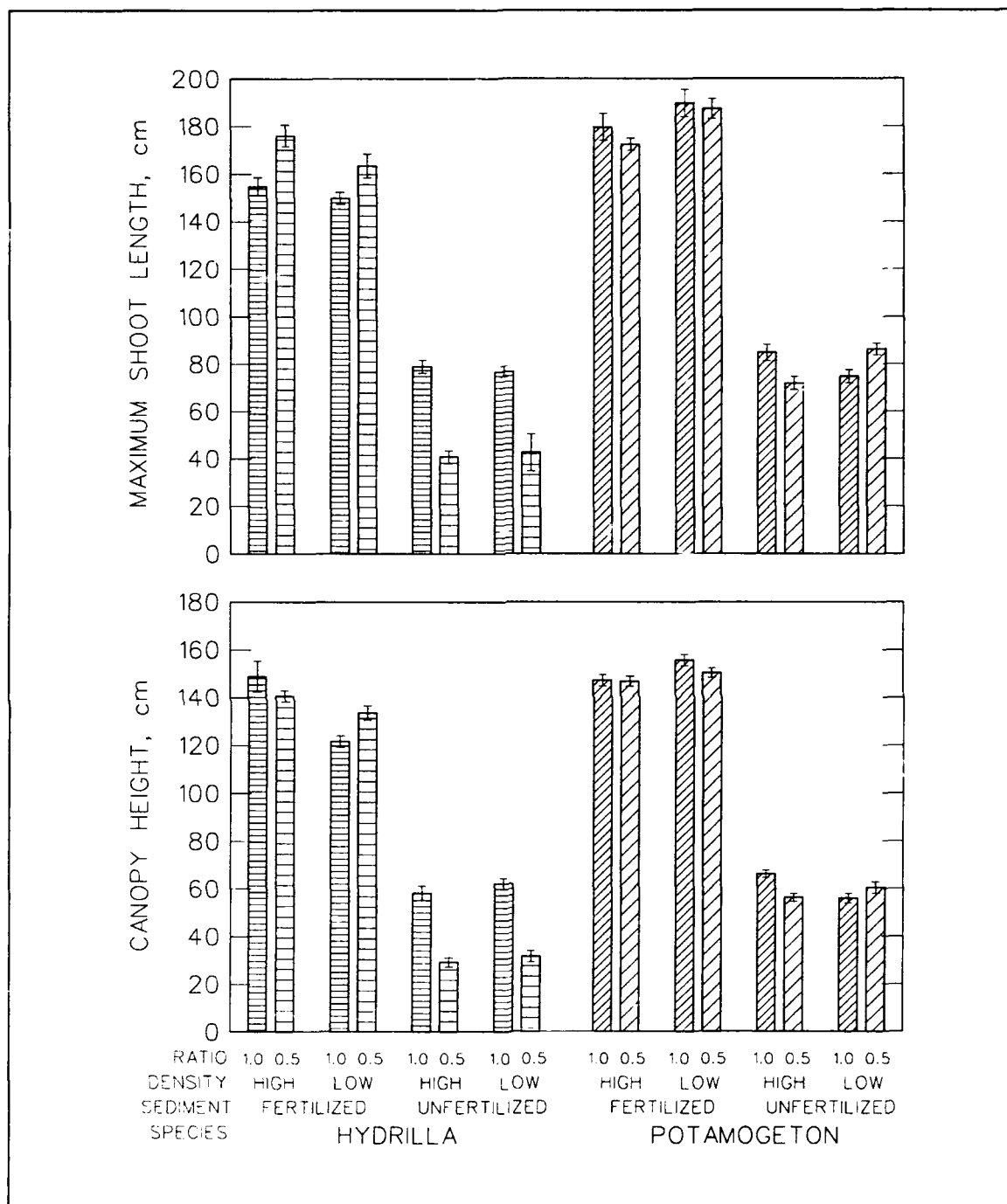
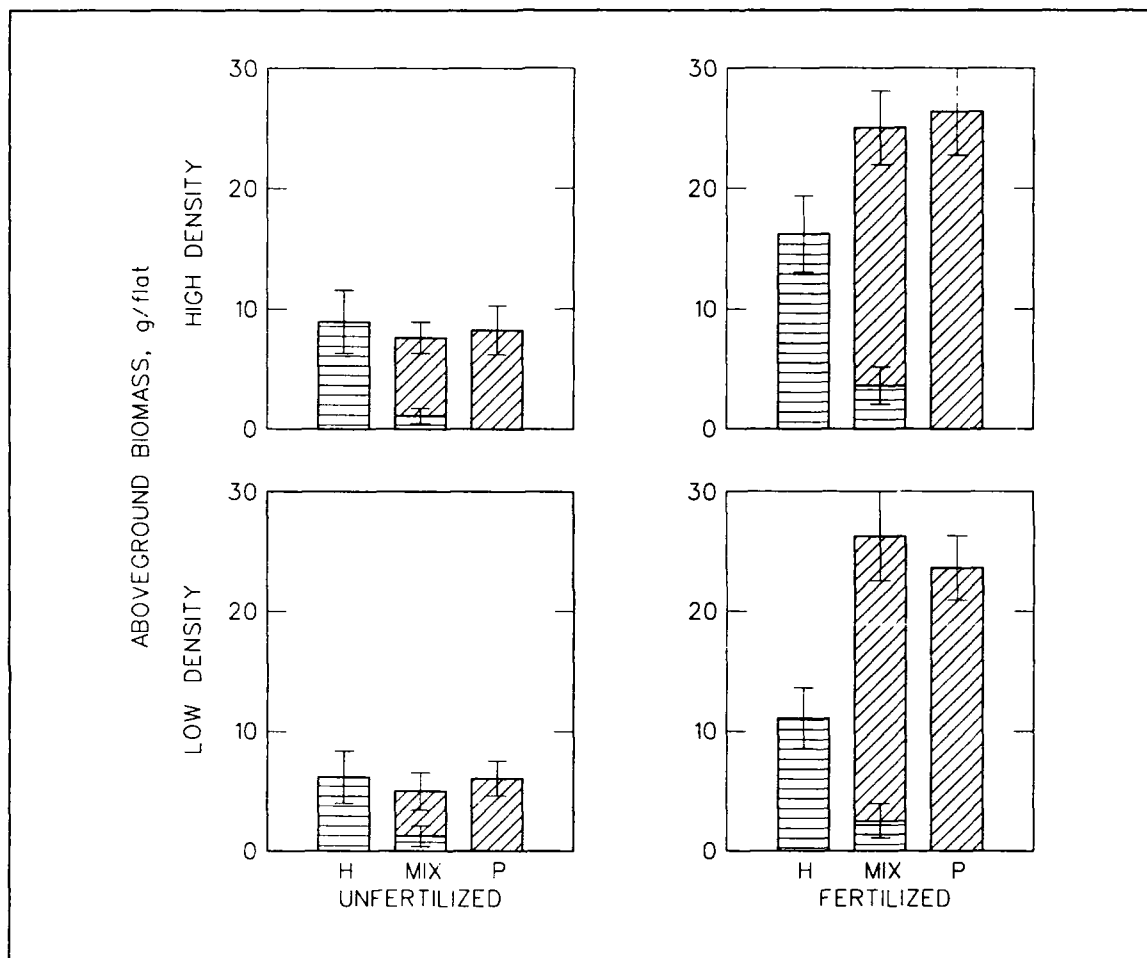Figure 2. Maximum shoot length (top panel) and canopy height (bottom panel) of *Hydrilla* and *Potamogeton* grown on fertilized or unfertilized sediment. Canopy height was determined as the midpoint of the most dense 10-cm segment of plant shoots. Ratios of 1.0 indicate monoculture responses, while ratios of 0.5 indicate mixture responses at both high (n = 16) and low (n = 8) initial plant density. Each bar is the mean ±1 standard error of six replicate flats
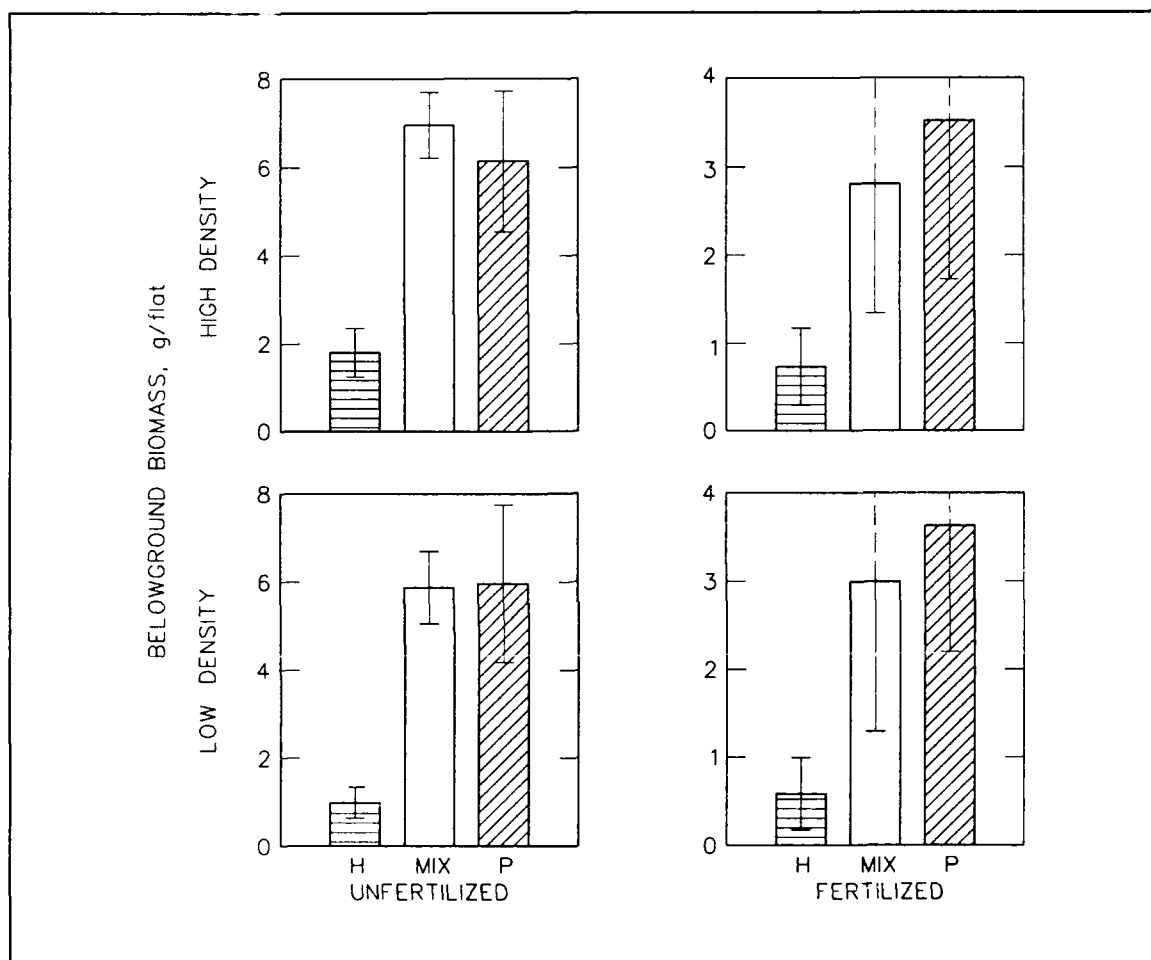
Figure 3. Aboveground biomass produced by *Hydrilla* (H) and *Potamogeton* (P). Responses to unfertilized sediment are indicated in the left panel, while responses to fertilized sediment are indicated in the right panel. The top panel presents responses to high initial plant density (n = 16); responses to low initial plant density (n = 8) are presented in the bottom panel. Horizontal stippling indicates *Hydrilla*'s contribution to biomass, while diagonal stippling indicates the contribution of *Potamogeton*. Each bar is the mean ±1 standard error of six replicate flats

Figure 4. Belowground biomass produced by *Hydrilla* (H) and *Potamogeton* (P). Responses to unfertilized sediment are indicated in the left panel, while responses to fertilized sediment are indicated in the right panel. The top panel presents responses to high initial plant density (n = 16); responses to low initial plant density (n = 8) are presented in the bottom panel. Stippling is used as in Figure 3, with biomass in mixtures (inseparable by species) presented as open bars. Values are estimated from approximately one half the total belowground biomass in a single flat. Each bar is the mean ±1 standard error of six replicate flats

Figure 5. Individual plant biomass of monospecifically grown *Hydrilla* (H) and *Potamogeton* (P) on fertilized or unfertilized sediments, at either high (n = 16) or low (n = 8) initial plant density. Each bar represents an average single plant ±1 standard error of six replicate flats, showing biomass allocation to aboveground (AG) and belowground (BG) structures. Plus sign denotes a significant difference in aboveground biomass between density treatments
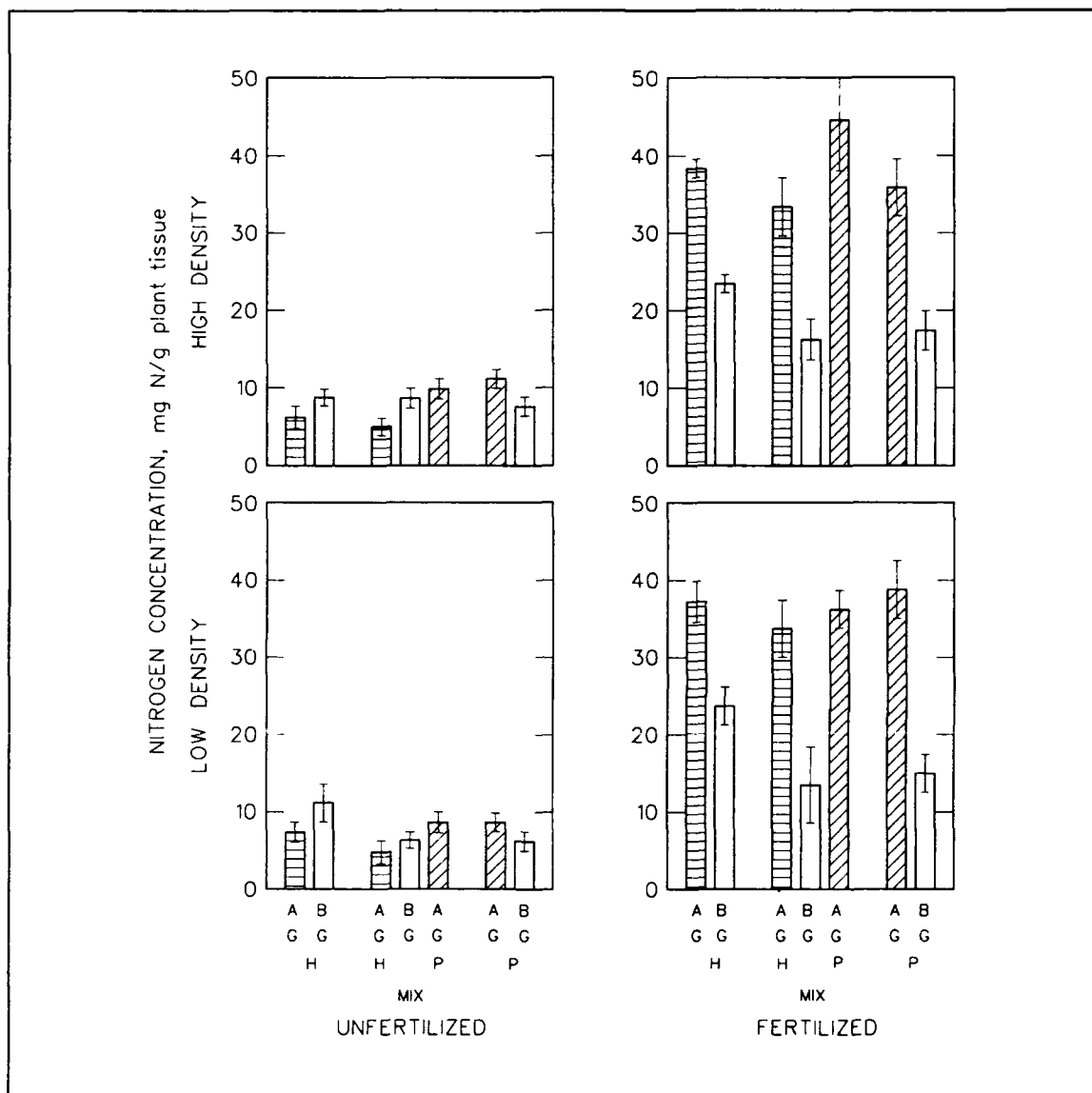
Figure 6. Nitrogen concentrations in tissues of *Hydrilla* (H) and *Potamogeton* (P). Horizontal stippling indicates aboveground (AG) tissues of *Hydrilla*, diagonal stippling indicates aboveground tissues of *Potamogeton*, and open bars indicate all belowground (BG) tissues. Responses to unfertilized sediment are indicated in the left panel, while responses to fertilized sediment are indicated in the right panel. The top panel presents responses to high (n = 16) inital plant density; responses to low initial plant density (n = 8) are presented in the bottom panel. Each bar is the mean ±1 standard error of six replicate flats. (For comparison, initial *Hydrilla* tissue N = 48.16 ± 6.14 mg N/g plant tissue; initial *Potamogeton* tissue N = 20.07 ± 1.14 mg N/g plant tissue)
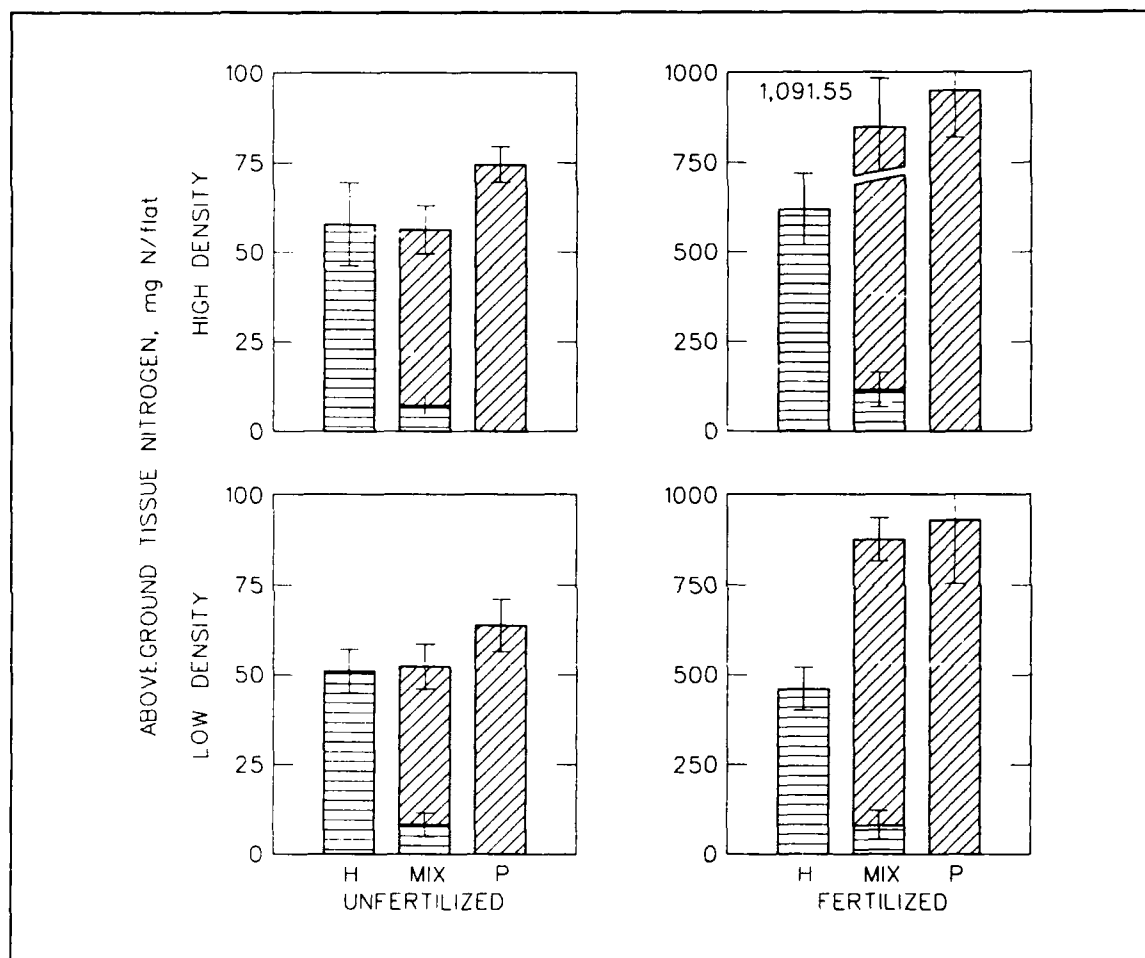
Figure 7. Total aboveground tissue nitrogen in *Hydrilla* (H) and *Potamogeton* (P). Responses to unfertilized sediment are indicated in the left panel, while responses to fertilized sediment are indicated in the right panel. The top panel presents responses to high initial plant density (n = 16); responses to low initial plant density (n = 8) are presented in the bottom panel. Horizontal stippling indicates *Hydrilla*'s contribution to total aboveground tissue nitrogen; diagonal stippling indicates the contribution of *Potamogeton*. Each bar is the mean ±1 standard error of six replicate flats
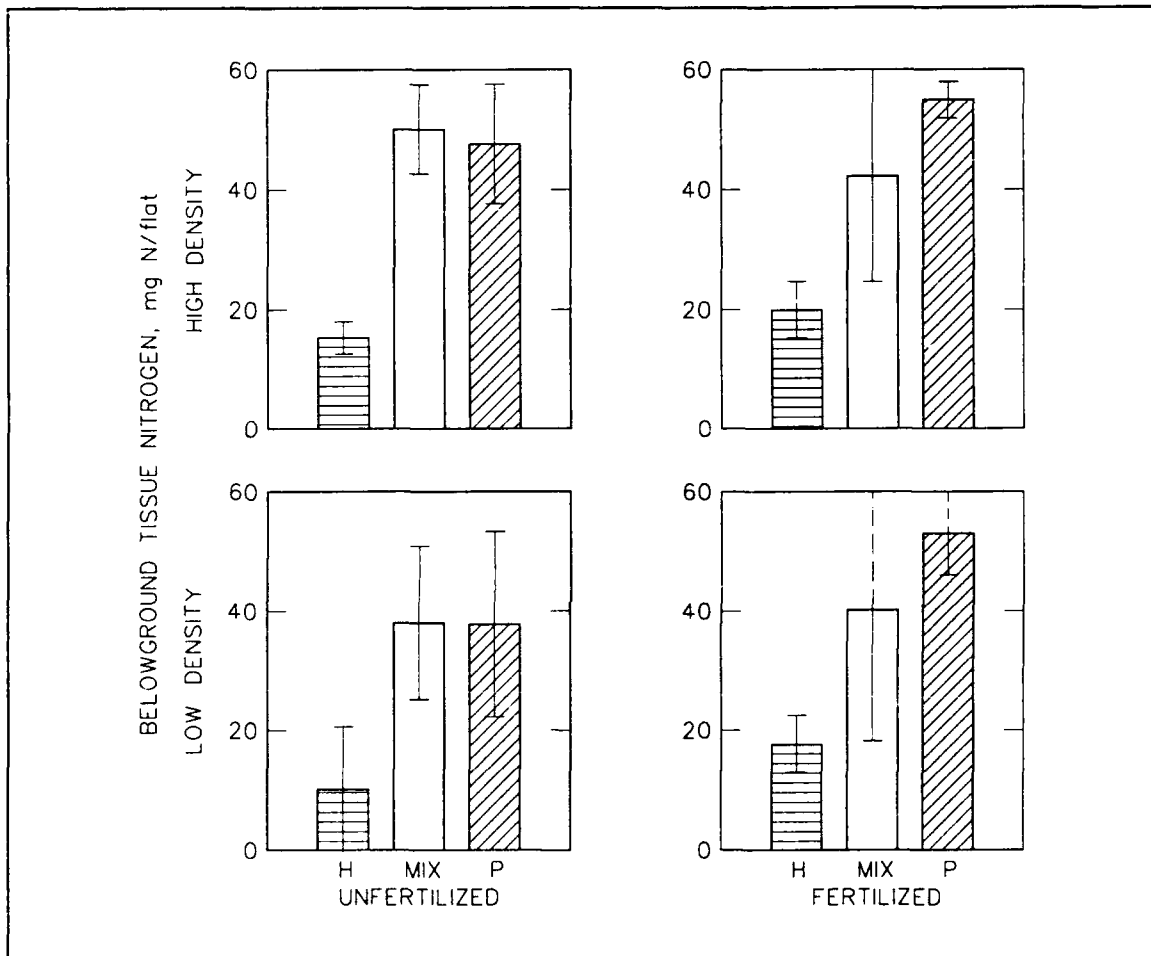
Figure 8. Total belowground tissue nitrogen in *Hydrilla* (H) and *Potamogeton* (P). Responses to unfertilized sediment are indicated in the left panel, while responses to fertilized sediment are indicated in the right panel. The top panel presents responses to high initial plant density (n = 16); responses to low initial plant density (n = 8) are presented in the bottom panel. Stippling is as used in Figure 7, with mixtures (inseparable by species) presented as open bars. Values are estimated from approximately one half the total belowground biomass in a single flat. Each bar is the mean ±1 standard error of six replicate flats
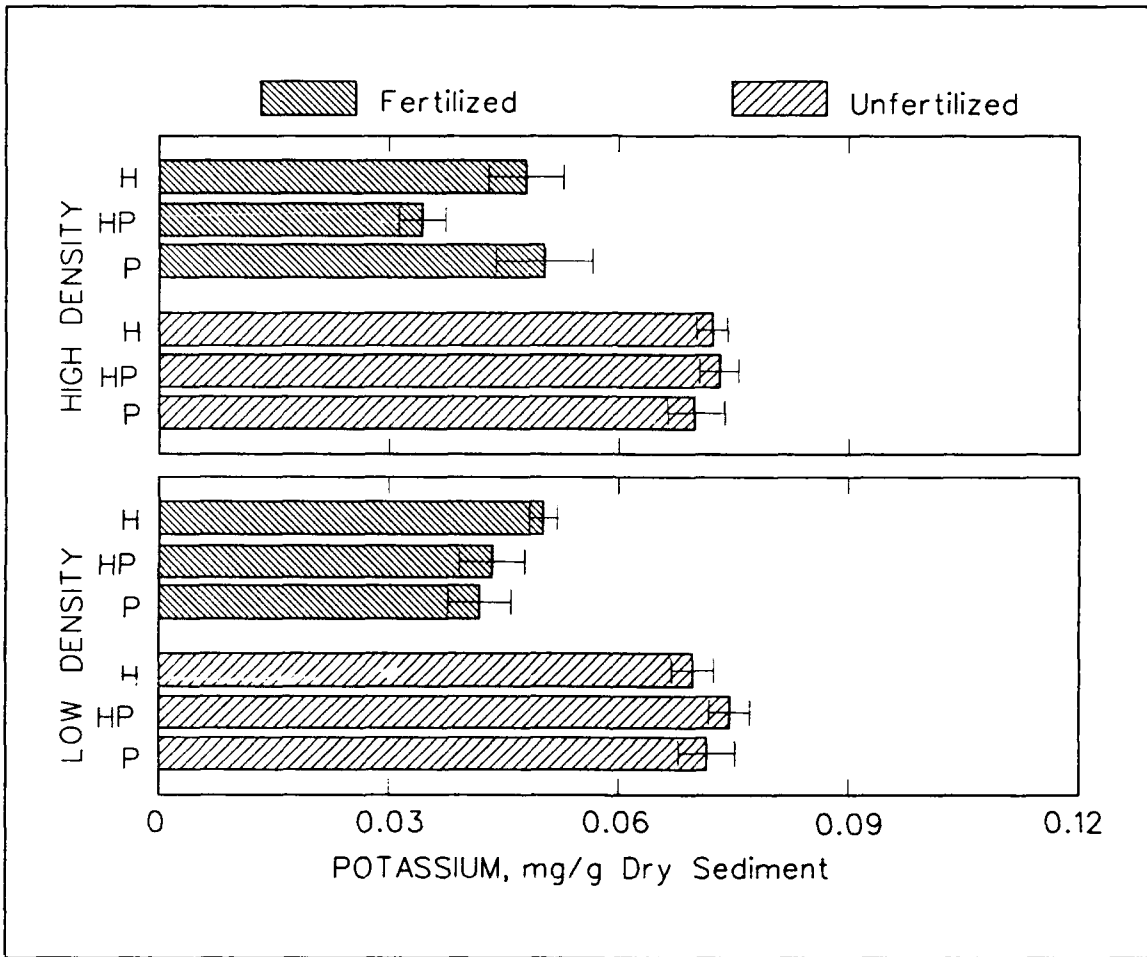
Figure 9. Final sediment exchangeable potassium, for fertilized and unfertilized sediments. The top panel presents responses to high (n = 16) initial plant density, with responses to low (n = 8) initial plant density presented in the bottom panel. Sediments supporting *Hydrilla* are indicated by H , those supporting *Potamogeton* are indicated by P , and those supporting mixtures of both species are indicated by HP . Each bar is the mean ±1 standard error of six replicate flats
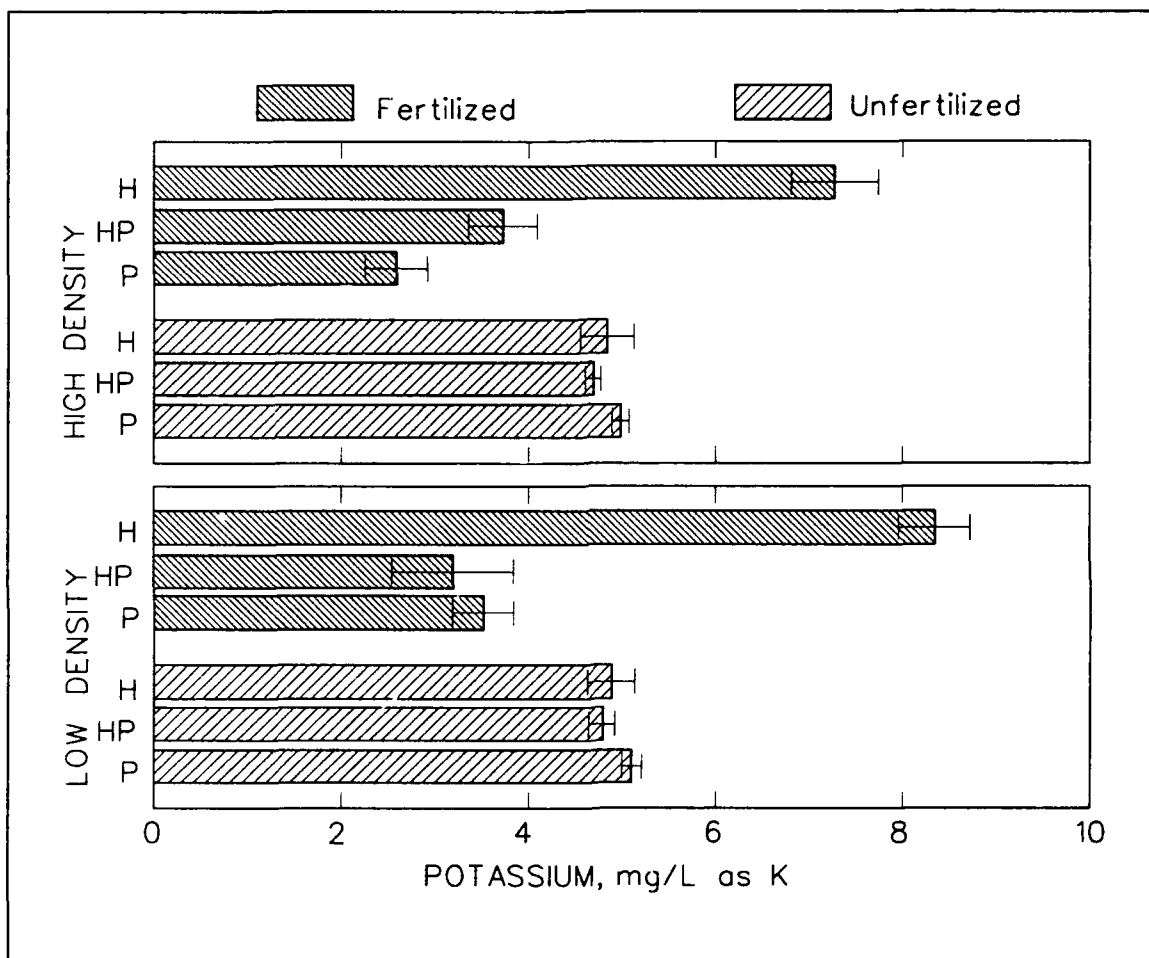
Figure 10. Final sediment interstitial potassium for fertilized and unfertilized sediments.
The top panel presents responses to high (n = 16) initial plant density, with responses to
low (n = 8) initial plant density presented in the bottom panel. Sediments supporting
Hydrilla are indicated by H , those supporting *Potamogeton* are indicated by P , and
those supporting mixtures of both species are indicated by HP . Each bar is the mean
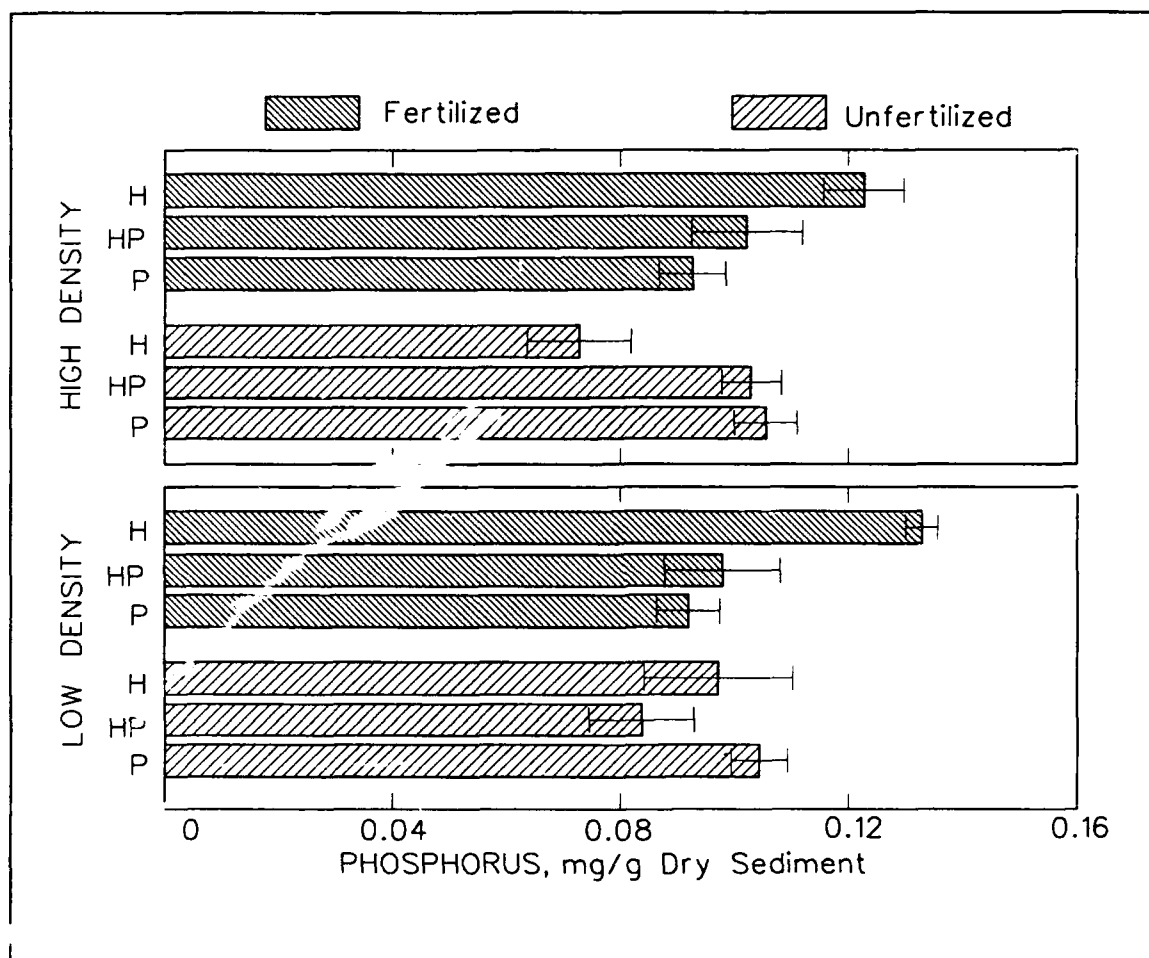±1 standard error of six replicate flats

Figure 11. Final sediment exchangeable phosphorus for fertilized and unfertilized sediments. The top panel presents responses to high (n = 16) initial plant density, with responses to low (n = 8) initial plant density prt sented in the bottom panel. Sediments supporting *Hydrilla* are indicated by H , those supporting *Potamogeton* are indicated by P , and those supporting mixtures of both species are indicated by HP . Each bar is the mean ±1 standard error of six replicate flats
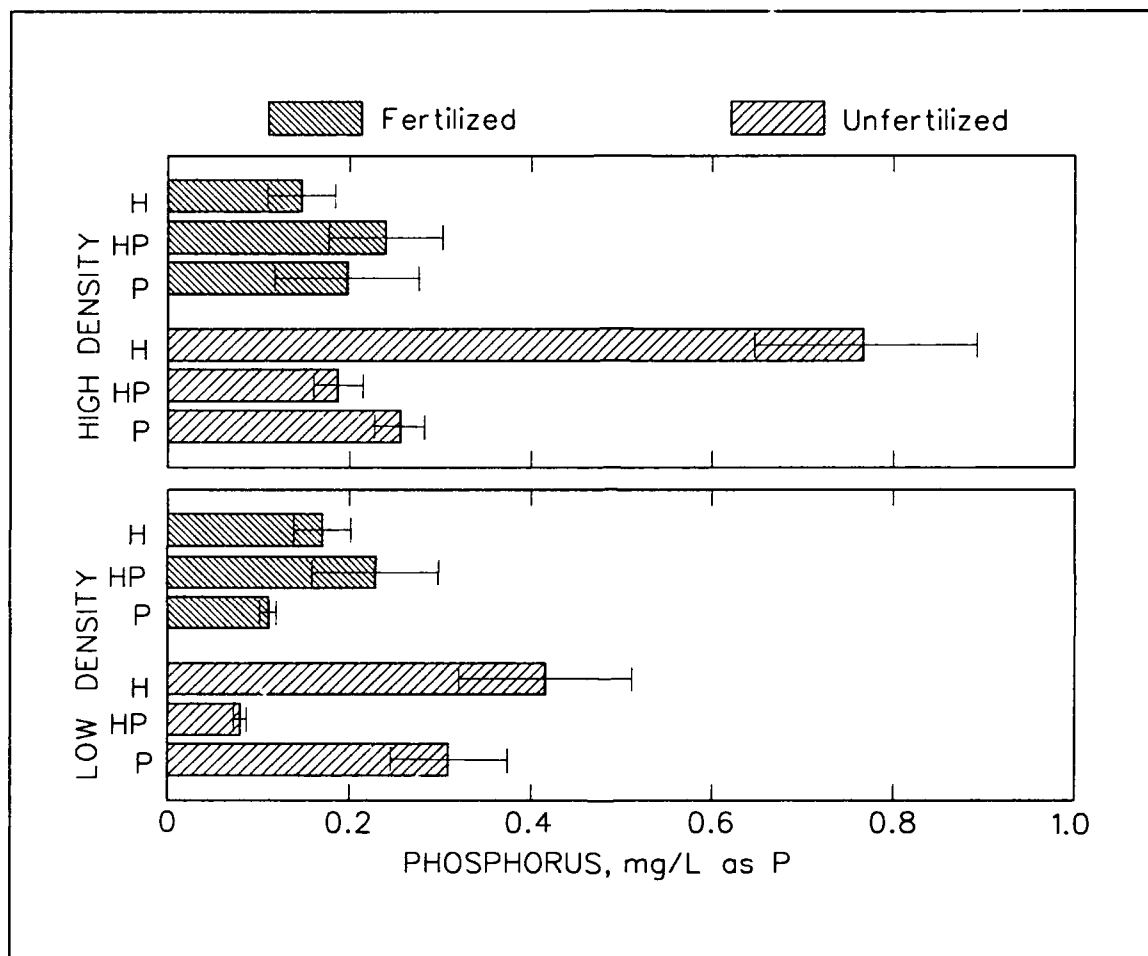
Figure 12. Final sediment interstitial phosphorus for fertilized and unfertilized sediments. The top panel presents responses to high (n = 16) initial plant density, with responses to low (n = 8) initial plant density presented in the bottom panel. Sediments supporting *Hydrilla* are indicated by H , those supporting *Potamogeton* are indicated by P , and those supporting mixtures of both species are indicated by HP. Each bar is the mean ±1 standard error of six replicate flats
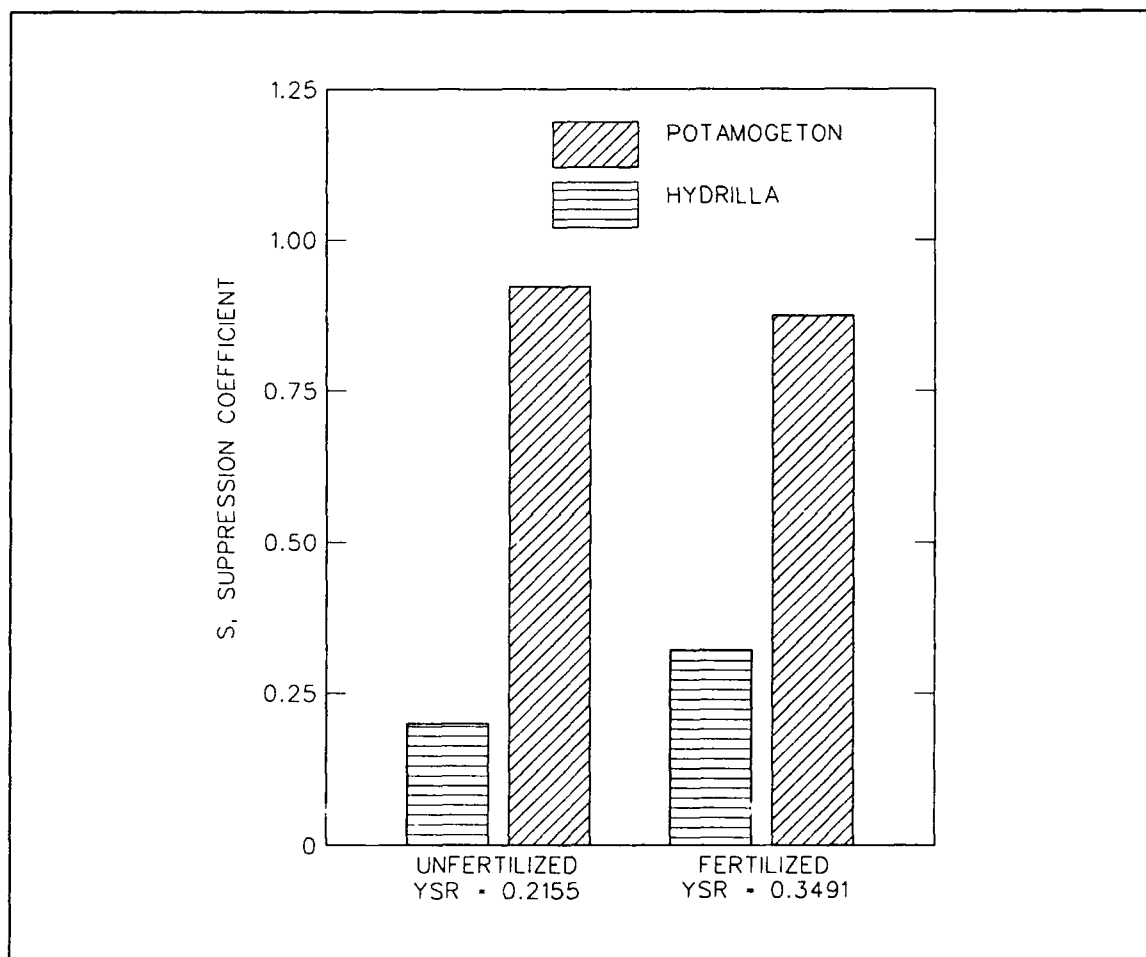
Figure 13. Suppression coefficients for *Hydrilla* and *Potamogeton* grown in mixtures on unfertilized or fertilized sediment (calculated after Aarssen 1985)

Table 1
Inflorescence Counts per Tank and Floating Leaves per Initial Plant of _Potamogeton americanus_ under High Sediment Fertility[1]

Response Variable	_Potamogeton_ Monoculture	50:50 Mixture
High Density		
Inflorescence count	7	24
Floating leaves per initial plant	17.9 (4.6%)	26.4 (6.2%)
Low Density		
Inflorescence count	19	41
Floating leaves per initial plant	26.5 (2.5%)	46.3 (4.5%)

[1] Values represent means (coefficients of variation); n = 6.

Table 2
Sediment Exchangeable Nitrogen (Measured as NH_4-N, Expressed in mg N/g Dry Sediment)[1]

Species Ratio	Low Density	High Density
Unfertilized Sediment (0.0115 ± 0.0003 mg N/g)		
Hydrilla	0.0026 ± 0.0003	0.0033 ± 0.0007
50:50 mixture	0.0031 ± 0.0005	0.0033 ± 0.0005
Potamogeton	0.0035 ± 0.0006	0.0031 ± 0.0004
Fertilized Sediment (0.2107 ± 0.0049 mg N/g)		
Hydrilla	0.0882 ± 0.0331	0.0488 ± 0.0410
50:50 mixture	0.0127 ± 0.0107	0.0137 ± 0.0195
Potamogeton	0.0084 ± 0.0052	0.0067 ± 0.0010

[1] Values are means of six replicates ± standard deviation, with mean initial values (n = 6) presented parenthetically.

Table 3
Sediment Interstitial Nitrogen (Measured as NH_4-N, Expressed in mg N/L Interstitial Water)[1]

Species Ratio	Low Density	High Density
Unfertilized Sediment (1.8667 ± 0.0509 mg N/L)		
Hydrilla	0.1633 ± 0.0739	0.1767 ± 0.0807
50:50 mixture	0.1300 ± 0.0335	0.1267 ± 0.0855
Potamogeton	0.1133 ± 0.0151	0.1267 ± 0.0186
Fertilized Sediment (92.2667 ± 4.4261 mg N/L)		
Hydrilla	26.6833 ± 7.4813	16.9500 ± 5.5479
50:50 mixture	2.7750 ± 3.6415	2.3117 ± 3.0237
Potamogeton	1.1550 ± 1.0260	0.4600 ± 0.3339

[1] Values are means of six replicates ± standard deviation, with mean initial values (n = 6) presented parenthetically.